

THE ROLES OF SEASONALITY, HOST SYNCHRONY, AND BEHAVIOUR IN THE EVOLUTIONS AND DISTRIBUTIONS OF NEST PARASITES IN HYMENOPTERA (INSECTA), WITH SPECIAL REFERENCE TO BEES (APOIDEA)

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"Come, poor Bee! Throw aside your exhausting labours, follow the evolutionists' advice and, as you have the means at your disposal, become a parasite!"

J. H. Fabre (1914), *The Mason Bees*

I. INTRODUCTION

In a world where advice from naturalists like Fabre might be meaningful, some good advice to a bee (or wasp or ant) trying to "become parasitic" is to reside in a seasonal area. This paper shows that there are proportionally more clepto- and social parasitic species of bees (Apoidea), wasps (Vespoidea, Sphecoidea), and ants (Formicoidea) [Hymenoptera] in temperate regions than nearer the equator. Parallel geographic

variation in the degree to which the ontogenetic development of potential hosts (individuals or colonies) is synchronized within and among populations helps explain the distributions of their parasites. In some areas (e.g. xeric or temperate regions) there are periodically harsh conditions which impose stabilizing selection on individuals so that their life histories are relatively synchronized to the favourable period, and nests are predictably abundant in time. This synchronization is imposed by seasonal environments and is also important for parasitic relationships in other animals (sections III and X).

For parasites, the probability of locating an appropriate host (at a suitable life-cycle stage) will be higher in seasonal versus aseasonal areas, as host abundance becomes increasingly predictable in time. A local abundance of individuals may intensify competition for any limited resources necessary for reproduction (Alexander, 1974; West-Eberhard, 1981), *creating* a social environment favourable for intraspecific parasitic behaviour, suggesting that the origins of parasitic behaviour are also associated with synchrony of the life-cycles of host individuals.

II. EXPLANATION OF TERMS AND GENERALIZED LIFE HISTORIES

Bees, wasps and ants which dig or construct nests are the potential *hosts*. Host species may be solitary or social. After establishing a nest, the nesting female(s) gather food (pollen, other insects, etc.) and store it in the nest, or feed it to developing offspring. When these offspring become adults, the females initiate new nests if they are solitary. If social, the females either remain at the natal nest to help rear siblings, or become replacement queens; in other species females form a swarm to initiate a new nest. The resources which are stockpiled in the nest (stored food, brood, or a group of workers) are stolen and used *in situ* by *parasites*. Numerous terms have been used by different authors (see Wheeler, 1910; Wilson, 1971) for the various kinds of parasitism of social behaviour. As used here, *parasite* describes a female (*F*) which utilizes *in situ* the reproductive effort of a non-related female(s) to rear her (*F*) offspring with a net cost to the host female(s).

A *usurping* female forcefully displaces another hetero- or conspecific female(s) from a nest constructed by the latter, and then uses that nest to rear offspring. Any resources other than the physical structure (e.g. nutrients in brood to cannibalize – e.g. Kasuya, Hibino & Itô, 1980) make the robbery more valuable to the usurper. The original occupant is usually evicted or killed (Section VI).

A *cleptoparasite* enters a nest of a solitary or social host and deposits eggs in one to several cells (in bees and wasps) and then usually leaves the nest to search for others or returns later. In some species the adult parasite kills the host larvae, while in others the parasite larvae have stages with specialized scythe-like mandibles for killing host or other parasite larvae. The parasite larvae feed on the provisions stored by the host female for her offspring (Section VI).

A *social parasite* (*inquiline*) enters the nest of a social host, either kills or dominates the reigning queen, and lives socially within the colony, in effect replacing the host queen. The parasite diverts the labour of the host workers causing them to rear her offspring. Social parasitism may be temporary or permanent, and facultative (occasional) or obligatory (essential for reproduction) (section VI).

Dulosis ('slavery') in ants (Myrmicinae and Formicinae; Formicidae) is often treated

as a kind of parasitism (e.g. Wilson, 1971), but will only be briefly mentioned here. The resources stolen by these ants are the brood of other colonies (con- or heterospecific), and are not exploited *in situ*, so the evolutionary origins of dulosis may be more 'predatory' than 'parasitic', as suggested by Darwin (1859) and others (e.g. Wilson, 1971; Stuart & Alloway, 1982). This behaviour has parallels in the robbing behaviour of tropical stingless bees (Meliponinae) and honey bees (*Apis*) (Nogueira-Neto, 1970; Sakagami, 1982; Koeniger, 1982; Seeley, 1985). Two meliponine genera (*Lestrimelitta* and *Cleptotrigona*), and possibly a third (*Trichotrigona*) as suggested by morphology (Camargo & Moure, 1983), are often considered as parasites. These bees are obligate robbers with a functional worker caste which build a nest. The stolen resources are also not used *in situ* (Sakagami, 1982; Wille, 1983).

III. FACTORS RELATED TO THE ORIGINS AND EVOLUTIONS OF PARASITIC BEHAVIOUR

Following a review of usurpation and cleptoparasitism in spider wasps (Pompilidae), Crèvecoeur (1931) noted that the frequency of 'thievery' (*brigandage*) seemed to be density-dependent, and Fabre (1914) described similar observations for bees (Apoidea) (Section VI). The success of other insect parasitoids is sometimes partially dependent upon host density, and sometimes inversely dependent (Lessels, 1985). Natural history observations, as well as experimental studies (Section IV), suggest that successful parasitism in bees, wasps and ants is in part density-dependent.

In addition to spatial density, the temporal density of hosts is also important for parasites. Seasonal limitations on the life-cycles of individuals or colonies of nesting Hymenoptera (hosts) influence both the origins and maintenance of social and cleptoparasitic behaviour for the following reasons:

(1) Synchronized emergence of individuals is usually induced by the onset of a period favourable for reproduction, which is then followed by an unfavourable period (Tauber, Tauber & Masaki, 1986; Wolda, 1979). In seasonal areas, stabilizing selection eliminates early and late emerging (free-living) females, so that the ontogenies of most individuals are synchronized to the favourable season (Schmalhausen, 1949). In these regions the favourable period ends more or less abruptly, and any free-living individuals which emerge late from diapause, have their nest destroyed, or otherwise get a late start, may rear fewer or no reproductive offspring because of the shortened nesting season (Section X).

(2) The number of hosts available to an obligate or facultative parasite increases as the ontogenies of individuals (or colonies) become increasingly synchronized within the host population. In other words, during predictable periods there are more 'suitable' hosts to attack, assuming total population sizes are more or less equal (also Starr, 1979). The importance of this relationship was discussed by both Janzen (1981) and Gauld (1986) in studies showing a greater diversity of parasitic ichneumon wasps (Hymenoptera, Parasitica) in temperate areas (also Vecht, 1953; Doult, Annecke & Tremblay, 1976). The relationship between ontogenetic synchrony and 'temporal density' is well-known in birds as 'the Fraser Darling effect' (Darling, 1938; Lack, 1968) and is thought to be important for the evolution of brood parasitic birds (Section X). Insects on host plants provide another convergent example of the general importance of host synchrony for parasites. Species-richness in treehoppers (Homoptera, Membracidae) appears to be lower in the Neotropics relative to temperate

regions, which is attributed to reduced co-ordination of treehopper life-history with the phenology of host plants in neotropical regions (Wood & Olmstead, 1984).

(3) Within highly synchronized populations competition for limited resources (e.g. nests or nesting sites) may be more intense (Richards, 1927; Alford, 1975; Sakagami, 1976; Archer, 1985). At high population densities, other nests are easily located so that 'losers' in social competitions, including females whose nests are destroyed by predation, may attempt to parasitize others to still produce some offspring, if they are physiologically competent to produce eggs. *Inhibition* of oocyte resorption (see Bell & Bohm, 1975) may occur in a facultative parasite, possibly representing one proximate mechanism for the origins of parasitic behaviour (Section VII).

In the following sections I discuss these relationships and how they can help explain why parasitic behaviour as a species character (Sections VIII and IX) follows a latitudinal cline, although the behavioural antecedents are widespread and may or may not do so (Section IV).

IV. FACULTATIVE PARASITIC BEHAVIOUR

Wheeler (1923) viewed the whole organic world as "burdened with parasitism," and there are examples of facultative parasites from many populations of otherwise free-living solitary or social bees, wasps and ants (Table 1). The relative frequency of this behaviour in different areas is unknown. Since it requires little or no evolutionary innovation beyond existing social behaviour, it may not be as regional as obligate parasitism (Sections VIII and IX).

Paper wasps (*Polistes*) are well-known facultative parasites, and usually their behaviour is similar to the 'social' behaviour that dominant females display towards subordinates (Yoshikawa, 1962; West-Eberhard, 1969; Makino, 1985). In *Polistes metricus* (Vespidae) in northeastern Kansas USA (39° N), experimental manipulations of nest density showed that nest usurpation occurred more frequently at higher population densities, even though there were abundant unoccupied nest boxes (Gamboa, 1978).

A common assumption is that competition for nesting sites is a primary contributor to the evolution of parasitic behaviour in the Aculeata (Richards, 1927, 1949; Taylor, 1939; but Andersson, 1984, for birds). Archer (1985) suggested that competition among gynés of *Vespula* for nesting sites is responsible for some observed periodic cycles in population densities in England, and suitable sites are also sometimes limited for bumblebees (*Bombus*) (K. W. Richards, 1973). For many solitary ground-nesting bees and wasps, however, suitable nesting sites are not a limiting factor (Wcislo, 1984). The usurped nest and what it may contain is more valuable as a resource than is the nesting site *per se* (Yamane, 1978; Matsuura & Yamane, 1984).

Facultative parasitic behaviour in social ants has been known since Huber's (1810) studies, and has been excellently reviewed (e.g. Wheeler, 1910; Stumper, 1950; Wilson, 1971; Elmes, 1982). Queens of *Formica* spp., for example, will sometimes invade already established colonies instead of founding their own. The invader usually kills the host queen(s) and utilizes the host workers to rear her own brood (references in Wilson, 1971).

Table 1. Representative examples of facultative parasitic behaviour within otherwise free-living species of Hymenoptera (Insecta)

(This list is not an exhaustive survey. The resources which are parasitized are indicated as follows: 1 = nest or nest cell(s); 2 = provisioned food; 3 = workers or brood.)

Species	Locality	Resources parasitized	Reference
Apoidea			
<i>Halictus malachurus</i>	France	1, 2	Plateaux-Quénu (1960)
<i>H. scabiosae</i>	France	1, 2	Knerer & Plateau-Quénu (1967)
<i>H. ligatus</i>	Florida, USA	1, 2?	Packer (1986a)
<i>Lasioglossum zephyrum</i>	Kansas, USA	1, 2	Batra (1966)
<i>L. aeneiventris</i>	Costa Rica	1, 2?	Wcislo <i>et al.</i> (in prep)
<i>Agapostemon virescens</i>	New York, USA	1	Abrams & Eickwort (1981)
<i>Apis mellifera ligustica</i>	Japan	1, 2	Sakagami (1959)
<i>A. mellifera scutellata</i>	Latin America	1, 2	Michener (1975b)
Various <i>Bombus</i> spp.	Holarctic localities	1, 2, 3	See Richards (1927); Sakagami (1976)
<i>Osmia californica</i>	Utah, USA	1	Bohart (1955)
<i>Hoplitis anthocopoides</i>	New York, USA	1, 2	Eickwort (1975)
<i>Megachile coquillettii</i>	California, USA	1	Eickwort (1985)
<i>M. aliceae</i>	Meaklip, South Africa	1	Gess & Gess (1986)
<i>Eucera difficilis</i>	Japan	1, 2?	Masuda (1940)
<i>Xylocopa pubescens</i>	Israel	1	Velthuis & Gerling (1983)
Various <i>Xylocopa</i> spp.	Southern Africa	1	See Watmough (1983)
<i>Ptiloglossa arizonensis</i>	Arizona, USA	1, 2	Rozen (1984)
Sphecoidea			
<i>Clypeadon lactincinctus</i>	Colorado, USA	2	Alexander (1986)
<i>Stictia heros</i>	Costa Rica	2	Sheehan (1984)
<i>Trigonopsis cameranii</i>	Cali, Colombia	2	Eberhard (1974)
Various <i>Trypoxylon</i> spp.	England	1	See Danks (1971)
<i>Trypoxylon politum</i>	Florida, USA	1, 2	Brockmann (1980)
<i>Monobia quadridens</i>	Kansas, USA	1	Byers (1972)
<i>Crabro monticola</i>	Minnesota, USA	1	Alcock (1982)
<i>C. cribrellifer</i>	Michigan, USA	1	Wcislo <i>et al.</i> (1985)
<i>Ammophila harti</i>	New York, USA	1?, 2	Hager & Kurczewski (1986)
Various Sphecoid wasps	Holarctic localities	1, 2	See Brockmann & Dawkins (1980)
Twig-nesting aculeates	Eastern USA	1, 2	See Krombein (1967)
Pompiloidea			
<i>Pompilus plumbeus</i>	Belgium	2	Crèvecoeur (1931)
<i>P. rufipes</i>	Algeria	2	Ferton (1923)
<i>Auplopus semialatus</i>	Costa Rica	1, 2	Wcislo <i>et al.</i> (in press)
Various pompilid species	England	1, 2	See Richards & Hamm (1939)
Vespoidea			
<i>Polistes biglumis</i>	Sapporo, Japan	1, 2, 3	Makino (1985)
<i>P. fadwigae</i>	Japan	1, 3	e.g. Yoshikawa (1955)
<i>Vespa dyboskii</i>	Japan	1, 3	Sakagami & Fukushima (1957)
<i>V. crabro</i>	France	1, 2, 3	Janet (1895)
<i>V. crabro</i>	Japan	1, 2, 3	Matsuura (1970)
Various <i>Vespula</i> spp.	Holarctic regions	1, 3	Archer (1985)
<i>Dolichovespula arenaria</i>	New York, USA	1, 3?	O'Rourke & Kurczewski (1984)
<i>D. arenaria</i>	Ontario, Canada	1, 3	Pallett (1984)
<i>Parishnogaster nigricans</i>	Java	1, 3	Turillazzi (1985)
<i>P. mellyi</i>	Thailand	1	Hansell (1983)
<i>Ropalidia plebeiana</i>	Australia	1, 2?	Itô (1985)
<i>Metapolybia cingulata</i>	Ecuador	?	Forsyth (1975)
Formicoidea			
Various <i>Formica</i> spp.	Europe, USA	1, 2, 3	See Wheeler (1910); Wilson (1971)

V. LOCATING HOSTS AND ONTOGENETIC SYNCHRONY IN HOST POPULATIONS

Parasites will usually be rare or absent when or where hosts do not live. For example, a twig-nesting bee, *Macrogalea candida* (Anthoporidae), is free-living and widely distributed, yet uncommon, throughout most of tropical Africa. This species is, however, commonly collected along the east coast of Tanzania and Kenya, which is the only area where its parasite, *M. mombasae*, is known; these are the only two species of *Macrogalea* known from Africa (Michener, 1970, 1971, 1975).

The distribution of hosts has a temporal component as well as a spatial one, and the relative importance of the former to parasites depends in part on the duration of the period favourable for host reproduction (nest founding). The following factors will be considered when plotting the latitudinal distribution of parasitic behaviour.

(1) To what extent is (reproductive) nest-founding in bees, ants and wasps seasonal (=predictable in time), and to what extent does such seasonality vary with latitude? and

(2) Where seasonal, to what extent is nest-founding synchronized within the reproductive season?

This section shows that the life cycles of individuals in temperate populations are more synchronized than are those in tropical regions (for other parasitic insects, see Section III). In natural populations there is a continuum between 'synchronous' and 'asynchronous' life-cycles. As used in this paper the latter term refers to host populations in which nests at all stages of development (ontogeny) can be found throughout the year, while in 'synchronized' populations successful nests are only established near the beginning of the favourable period, and this period ends more or less abruptly.

Many variables not necessarily related to latitude also influence seasonal activity. It is relevant, however, that *all* examples of aseasonality are from tropical or subtropical populations. In some regions pronounced wet/dry seasons impose considerable synchrony on some aculeate species (e.g. Michener, 1954; Wille & Orozco, 1970; Evans & Hook, 1982; Brooks & Roubik, 1983), especially those which feed on floral resources or insect larvae. Near Brasilia, Brazil (15° S), for example, of 33 species of solitary bees, 23 species show distinguishable seasonal peaks in abundance, while 10 species do not (A. Raw, pers. comm.).

(a) *Ants*. The seasonal and diel timing of mating flights and colony founding in ants is often remarkably synchronized (e.g. Wheeler, 1906, 1910; Brian, 1965, 1977; Wilson, 1971; Higashi, 1983; Hölldobler & Bartz, 1985; Andersen, 1986). As a convergent example demonstrating the importance of 'host' synchrony, there are Nearctic species of sphecids wasps (*Aphilanthops*) which prey on a few related species of ants, taking only alates as they fly on their mating flights (Bohart & Menke, 1976; Evans & West-Eberhard, 1970). Colony founding in some tropical ants is seasonally periodic (e.g. Kanno, 1969; Wilson, 1971; Baldrige, Rettenmeyer & Watkins, 1980), while many tropical ants have asynchronous brood cycles and mating flights (e.g. Wilson, 1959, 1971; Brian, 1965).

(b) *Wasps*. Female paper wasps (*Polistes*) (Vespidae) that survived winter began nesting during the second week of May near Ann Arbor, Michigan, USA (42° N) (West-Eberhard, 1969), and also in early May at Kherson, USSR (46° N) (Grechka &

Kipyatkov, 1983). Closer to the equator near Cali, Colombia (4° N, West-Eberhard (1969) observed "little (if any) seasonal synchrony in the foundation and termination of *P. canadensis* (= *P. erythrocephalus* and *rufuscatus*) colonies". She also discussed factors which decreased the "likelihood of coincidental synchrony" among local populations. Evans & West-Eberhard (1970) generalized this to *Polistes* in aseasonal tropical areas, while in seasonal tropical places nest-founding in polistines is somewhat synchronized (Windsor, 1977). Polybiine wasps have seasonal reproductive cycles in tropical latitudes (5–20° N, 12–35° S), yet there is little synchrony *within* the reproductive season (West-Eberhard, 1982; Simões & Mechi, 1983; Gadagkar *et al.*, 1982). A polybiine wasp (*Parapolybia indica*) in a more seasonal region, near Tsu, Japan (34° N), began nesting only during the first 2–3 weeks of May (Sugiura, Sekijima & Matsuura, 1983). There are many examples of hornet and yellowjacket wasps (Vespinæ) that have synchronized nest-founding in temperate regions (e.g. Brian, 1965, 1977; Spradberry, 1973; Matsuura, 1984; Archer, 1985), while nest-founding in a tropical Sumatran vespid occurs throughout the year (Matsuura, 1985).

(c) *Bees*. The reproductive cycles of bees are closely linked with the availability of pollen and nectar from angiosperm flowers (Michener, 1974; Thorpe, 1979). O'Neil & Waller (1984) reviewed seasonal surveys of pollen intake into honey bee (*Apis*, Apidae) colonies from apiaries at several latitudes in North America (50.1–30.3° N). Honey bees are polylectic (= 'pollen generalists') and this measure is assumed to reflect resources available for rearing brood. Going from north to south there is a progressively less dramatic 'burst' of pollen availability: it is available for more months of the year in the south. Honey bees have a distinct reproductive swarming season in temperate areas (Seeley, 1985), while in some tropical areas swarming is less synchronized and swarms are produced over a much longer time period (Otis, 1982; M. Spivak, pers. comm.).

Geographic variation in the variance of emergence phenologies of one widely distributed species of sweat bee, *Halictus ligatus* (Halictidae), demonstrates the association between nesting synchrony and latitude. In the northern part of its range in Canada (50° N) this species typically nests in dense aggregations and nest-founding by individual gynes is highly synchronized (Michener & Bennett, 1977; Packer, 1986b), as in populations in New York, USA (42° N) (Litte, 1977). In subtropical Florida (24° N) colonies are more or less active and produce gynes throughout the year (Packer & Knerer, 1986), which is probably also true for those in Trinidad, West Indies (10° N) and Cali, Colombia (4° N) where nests are not as densely aggregated (Michener & Bennett, 1977).

For bees (Apoidea), nest-founding is largely synchronized both in seasonal north temperate (e.g., Malyshev, 1935; Michener, 1974; Løken, 1977; McKay & Knerer, 1979) and south temperate regions (Moure & Sakagami, 1962; Garófalo *et al.*, 1981; Camillo *et al.*, 1983), and tends to be less synchronized closer to the equator (e.g. Michener, 1954; Michener & Amir, 1977; Michener, Breed & Bell, 1979; Sakagami, Laroca & Moure, 1967; Heithaus, 1979; Roubik & Michener, 1980, 1985; Raw, 1985; Wolda & Roubik, 1986).

VI. TEMPORAL ASPECTS OF SUCCESSFUL PARASITIC INVASION

Aculeate parasites that aggressively invade host colonies tend to be successful only when they attack colonies younger than certain ontogenetic stages. A colony vulnerable

to parasites is typically young, usually having a small number of workers, although sometimes large, well-established colonies are successfully parasitized (e.g. Wheeler, 1906; Sladen, 1912; Stumper, 1950; Scheven, 1958). The 'window of vulnerability' usually narrows as host colonies increase in size, which is why synchrony of individuals within host populations is important to parasites.

The phenologies of obligate parasites are co-ordinated with those of their hosts such that parasite species usually emerge later in a season relative to hosts (e.g. Robertson, 1926; Alford, 1975; Thorpe, Horning & Dunning, 1983; Baker, Kuhn & Bambara, 1985). This co-ordination is also known for facultative parasites. In bumblebees (*Bombus*), for example, in areas where several or many species occur sympatrically, there are more likely to be facultative parasites among those free-living species which emerge later in the season (in temperate regions) (e.g. Sladen, 1899, 1912; Sakagami, 1976; K. W. Richards, 1978). Co-ordinated phenologies probably ensure that potential hosts will have gathered and stored enough resources to support the parasite's offspring, and demonstrate the importance of a temporal relationship between hosts and parasites, as emphasized by Richards (1927, Section X).

Fisher (1984a) introduced females of a host-specific parasitic bumblebee (*Psithyrus citrinus*) into host nests (*Bombus*) with varying numbers of workers [these parasites dominate but do not kill the host queen]. In the absence of workers the success rate of invading parasites was 100%; it decreased linearly to 20% when the number of workers increased to >40. A similar relationship between the probability of successful invasion and number of workers present was also found for a facultative parasitic bumblebee, *Bombus affinis* (Fisher, 1987).

Cleptoparasites, as implied by their name, must parasitize cells before the host larvae have consumed too much food, lest there be insufficient stores to nourish adequately the parasites' larvae (e.g. Deleurance, 1945; Evans, Lin & Yoshimoto, 1953; Olberg, 1959). For these reasons, some cleptoparasites learn the locations of host nests, and return repeatedly to inspect them (below).

VII. PARASITIC BEHAVIOUR AND CORRELATED REPRODUCTIVE MODIFICATIONS

For parasites which forcibly invade host nests the generally narrow 'window' of host vulnerability described above implies that in seasonal areas appropriate hosts are found during a relatively short time. Any physiological or genetic changes which cause eggs to develop more rapidly, or which increase the number of eggs that mature simultaneously will allow a 'burst' of egg-laying at the appropriate time. Numerous authors (e.g. Robson & Richards, 1936; Schmalhausen, 1949; Mayr, 1963; Waddington, 1975; Piaget, 1979; West-Eberhard, 1986) have noted that changes in behaviour (e.g. free-living to parasitic) and physiology (Bownes, 1983; Ho, 1986) alter the social environment the individual experiences during ontogeny, which will influence (buffer or intensify) the effects of natural selection. The physiological modifications described above will probably be selected if the accompanying behaviour is parasitic, as true for morphological modifications associated with parasitic behaviour [see Michener (1970, 1978), Reed & Akre (1982), and Wilson (1984)].

Wheeler (1919) hypothesized that an 'urgency to oviposit' experienced by a female with a mature egg in her oviduct, but otherwise unprepared to be free-living (= without a provisioned nest), represents one source of variation for the evolution of parasitic

behaviour. This 'urgency to oviposit' summarizes diverse physiological changes associated with egg maturation (Adams, 1980), and there is suggestive evidence for such changes in both facultative and obligate parasites. Packer (1986a) studied facultative *intraspecific* parasitic behaviour in *Halictus ligatus* females, and showed that parasitic females had mostly developing oocytes, and were significantly *less* likely to resorb developing oocytes relative to queens and workers. In addition to these physiological changes, the 'cuckoo' females were intermediate in size between queens and workers, and displayed a 'trap-lining' form of search behaviour commonly observed in some obligate bee parasites (e.g. Graenicher, 1906, 1927; Michener, 1955; Rozen *et al.*, 1977). Some females of a free-living social pompilid wasp (*Auplopus semialatus*) are able to mature several eggs simultaneously (Wcislo *et al.*, in press), so they may experience an 'urgency to oviposit'. On one nest aggression among females and prey usurpation were frequent, and the ovarian cycles of reproductive females were synchronized so that several females had mature eggs at the same time.

At least in bees, obligate parasites have similar physiological modifications based on dissections. In some groups (e.g. *Psithyrus*) parasites have more ovarioles per ovary than do their non-parasitic relatives, and presumably their ancestors, allowing them to mature more eggs at a given time (Richards, 1927; Palm, 1948; Cumber, 1949; Iwata & Sakagami, 1966; Rozen, 1986; Wcislo, unpubl. data. Wasps: parasites and hosts have the same number of ovarioles – Kugler, Orion & Ishay, 1976). Additionally, some cleptoparasitic bees have a series of continuously developing oocytes in each ovariole (Iwata & Saakagami, 1966; Wcislo, unpubl. data), suggestive of the ovarioles of eusocial *Apis* (Snodgrass, 1956) or meliponine bees (Michener, 1974), or ants (Wheeler, 1910), but unlike ovarioles of some of their solitary relatives which mature only one egg at a time. The individual eggs laid by parasites are also proportionally smaller relative to host egg size (Iwata & Sakagami, 1966).

VIII. GEOGRAPHIC DISTRIBUTION OF OBLIGATE PARASITES

In contrast with facultative behaviour, obligate parasitic behaviour as a species character in bees, wasps and ants has a temperate-biased distribution given the available data.

(a) *Ants*. In 1910 Wheeler stated that parasitic ants are more abundant in temperate regions, especially in cool montane or arid areas, and almost 60 years later Wilson (1971) said the same. Wilson (1971) cautioned against attributing much significance to this trend and suggested that the relative dearth of parasitic ants in tropical regions may be an artifact of the little collecting done there. According to Kutter (1969), of the known species of social parasites in ants 27 % are in the Nearctic region, 56 % from the Palearctic region, and 17 % from the rest of the world. More recently Wilson (1984) stated that "something of a paradox has emerged" from the last 180 years of research on parasitic ants:

The greatest frequency of social parasites, both in new species discovered per year and overall percentage of ant species known to be parasitic, occurs in the north temperate zone and especially in the colder portions, where the smallest total ant fauna exists (p. 318).

(b) *Social wasps*. Most social wasps [Vespidae; Stenogastrinae, Polistinae] are primarily tropical or subtropical in distribution (Vecht, 1967; O. W. Richards, 1971,

1978; Jeanne, 1980; Matsuura & Yamane, 1984). The abundant neotropical polistine fauna has many very closely allied species nesting in sympatry (O. W. Richards, 1978). These are usually *polygynous* colonies within which many females are socially excluded from laying eggs via competition for reproductive status (e.g. Naumann, 1970; Richards, 1971; West-Eberhard, 1978, 1981). These conditions – intense intracolony competition in areas where closely allied species are nesting sympatrically – are presumed to be favourable for the evolution of parasitic lineages (e.g. Richards, 1927, 1971; Taylor, 1939; Wilson, 1971). Despite favourable conditions, to date there are no known tropical parasitic Polistinae. This finding is in accord with the present hypothesis because life cycles of tropical polistine colonies are usually not synchronized. It may be relevant that in temperate zone *Polistes* attempted parasitism is more often successful when the host colony is monogynous rather than polygynous (Gamboa, 1978; Klahn, 1979), possibly because on monogynous nests there are fewer defenders.

Three species of *Polistes* (*Sulcopolistes*) are parasitic, and have Palearctic distributions (Weyrauch, 1958; Beaumont & Matthey, 1945; Beaumont, 1958; Scheven, 1958; Akre, 1982). Rodrigues (1968) stated without evidence that there is a parasitic *Polistes* in Brazil (23° N); Bequaert (1940; cited in Wilson, 1971) also speculated that there may be one parasitic species from Africa (*P. macrocephalus*) and one from the United States (*P. perplexus*). The former is known only from a type specimen and there is no evidence for its being parasitic (J. Carpenter, *in litt.*); the latter is a synonym of the free-living *P. carolinus* (O. W. Richards, 1978). Zikán (1949; cited in Wilson, 1971) asserted there were 26 species of parasitic *Mischocyttarus* (Polistinae) in the neotropics. Richards (1971, 1978) examined the type specimens and, on morphological bases only, concluded that they are presumably variants of free-living species, and are not parasitic.

The subfamily Vespinae has a mostly temperate distribution, with some species common in tropical Asia (Vecht, 1967; Akre, 1982; Matsuura & Yamane, 1984). One species of *Vespa*, two species of *Vespula*, and three of *Dolichovespula* are parasitic, and all are from Holarctic areas (Weyrauch, 1937; Matthews, 1982; Yamane, 1978; Akre *et al.*, 1981). *Vespula squamosa*, a species distributed from eastern North America to Guatemala (15° N) is an obligate social parasite in the northern part of its range (42° N), but is facultatively free-living in the southern USA (32° N) (Gaul, 1947; MacDonald & Matthews, 1975, 1984). In Florida, USA, polygynous free-living colonies are known (Ross & Matthews, 1982). Unlike other vespine social parasites, the sting shaft of *V. squamosa* is not strongly recurved (Reed & Akre, 1982).

(c) *Solitary wasps*. Cleptoparasitic sphecids wasps occur in the genus *Stizoides* and the tribe Nyssonini (e.g. Olberg, 1959; Evans, 1966). These wasps are especially well-represented in temperate holarctic regions, and some genera are also fairly common in the neotropics (e.g. *Zanysson*) and temperate South America (e.g. *Perisson*, *Cresson*) (Pate, 1938; Bohart & Menke, 1976). In spider wasps (Pompilidae) several genera are cleptoparasitic (e.g. *Ceropales*, *Evagetes*), but these have been studied mostly in temperate regions (Ferton, 1923; Townes, 1957; Evans & Yoshimoto, 1962), and little can be said about the significance of their distribution.

There are no known parasitic species in any of the subfamilies of solitary Vespidae (Eumeninae, Masarinae, Euparagiinae), although facultatively parasitic behaviours are known (Table 1).

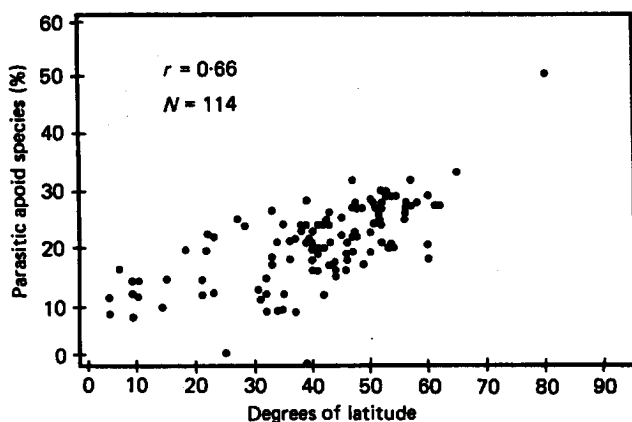


Fig. 1. The percentage of parasitic bees (Apoidea) in faunal surveys as a function of the latitude of the area surveyed.

IX. BIOGEOGRAPHY OF PARASITIC APOIDEA (BEES)

An example similar to *Vespa squamosa* (above) is found in a socially parasitic bumblebee, *Bombus hyperboreus* (Apidae). On Ellesmere Island in the arctic (80° N), and in other northerly areas of its distribution, only parasitic 'queens' have been collected (Milliron & Oliver, 1966; Richards, 1973; Pape, 1983). A few workers (but possibly small 'parasitic queens' – Michener, 1974) of this species are known from less northerly areas of its distribution in Fennoscandinavia (62–68° N) (Løken, 1973, 1977).

The data. In an attempt to quantify the abundance of parasitic species with respect to latitude and climate, I tallied the numbers of parasitic vs. nonparasitic species in all faunal surveys of bees available to me (Appendix 1). Surveys are mainly reports on general collecting of Apoidea in different regions. These surveys cover different-sized geographic areas and are of varying and often unknown quality with respect to the duration of the collecting as well as the assiduousness of the collector(s). For each survey ($N = 114$) the proportion of parasitic species collected to the total number of species collected, is plotted as a function of the estimated midpoint of the latitude of the area surveyed (Figure 1). A least-squares linear correlation between latitude and the proportion of parasitic species is $r = 0.66$. Janzon & Svensson (1984) collected bees on the island of Öland, Sweden (56° N) and reviewed some surveys from north temperate areas. The authors noted that in these areas the proportion of parasitic bee species remains at about 25–30%, as shown in Figure 1 for a larger data set. Free-living bee species are more abundant in temperate regions (Michener, 1979), which is also where parasitic bee species are more abundant. Free-living ants and wasp species, in contrast, are more abundant in tropical regions, yet parasitic species in these groups are still more abundant in temperate regions.

Some possible biases in the data. There is a systematic bias in these data because there has been more thorough collecting in temperate regions (see Michener, 1979). Poorly collected areas (e.g. most tropical regions) may have proportionally fewer parasites represented because parasites are usually rare and therefore less easily collected. Within

temperate regions, some areas which are well collected (e.g. Carlinville, Illinois, USA), as well as those which are poorly collected (e.g. Maine or New Jersey, USA) both fall within the observed trend, as does a well-collected bee fauna in the tropics (La Estacion de Biología Chamela, Mexico). These facts suggest that the observed pattern is not an artifact of a sampling bias. Comparing different surveys of the same area shows that the proportions of parasitic species are not significantly different despite additional collecting for Cuba, Chile, FDR, Belgium, and 'west Prussia' ($P \geq 0.05$, G-test). The proportion of parasitic species in France is significantly different between the two surveys ($0.025 > P > 0.01$, $G = 6.039$, G-test).

Historical biogeography. In addition to biological factors (Section VIII), history also influences present geographic variation in parasite species abundance. Australia, for example, is noteworthy for its depauperate parasitic apoid fauna, despite having an otherwise rich bee fauna, especially the short-tongued families Colletidae and Halictidae (Michener, 1965). There may be undescribed parasitic colletids because parasites in two of the subfamilies of Colletidae would be difficult to recognize, as *all* females lack external pollen-carrying scopae and carry pollen internally in their crops. The absence of scopae is often the simplest way to recognize parasitic bees, excluding 'queens' of social apids which also lack pollen-carrying structures. The only known supposedly parasitic colletids are five species of *Hylaeus* from Hawaii (Perkins & Forel, 1899). Among the hundreds of species of scopate colletids in Australia and elsewhere none shows signs of being parasitic (C. D. Michener, pers. comm.).

The historical biogeography of bees (Michener, 1979), in light of the phyletic distribution of parasitism in bees (see Popov, 1945; Bohart, 1970; Roubik, 1987), helps explain some of the above distributions. Bees (Apoidea) can be divided into two monophyletic groups, the long-tongued and short-tongued bees (Michener, 1944; Michener & Greenberg, 1980; Lomholdt 1982). Of the 187 genera of short-tongued bees (including Ctenoplectridae), 10 genera (5 %) contain parasitic species, while in the 229 genera of long-tongued bees 73 genera (32 %) have parasitic species (after R. Roberts, unpublished checklist). Robertson (1926, 1929) collected 296 species of bees near Carlinville, Illinois, USA, and of these 50.6 % are in the short-tongued families, and 49.4 % are in the long-tongued families. Of the parasitic species he collected, 77.7 % are long-tongued bees. Within long-tongued bees 38.3 % of the species are parasites, whereas only 10.6 % of the short-tongued bees are parasites. Much of the diversity of parasites seen in long-tongued bees is due to the radiation of the Nomadinae (Anthophoridae), especially *Nomada*. For surveys in which *Nomada* was present, bees in this genus accounted for 2-68 % of the parasitic bee fauna ($\bar{x} = 34.7$ %, $s = 13.1$, $N = 83$). With the exception of the Halictidae, which contains numerous parasitic lineages, the short-tongued bees have generated relatively few parasitic lineages, yet bees in these families serve as hosts for other parasites. Why short-tongued bees have generated relatively few parasitic lineages is unresolved.

Noting that the fossil record for bees is poor Michener (1979) speculated that bees arose from the sphecoid wasps at some time in the mid- to late-Cretaceous, perhaps in the interior of Gondwanaland. Assuming this to be true, then for biogeographical reasons, areas with *more* short-tongued bee lineages are expected to have *fewer* parasite species. The bee fauna of Australia is dominated by short-tongued bees, possibly because this continent (with Antarctica) split off from the rest of Gondwanaland before

the origin or major radiation of the long-tongued bees (see Michener, 1979). Among the long-tongued bees which do occur in Australia (e.g., Allodapini and Anthrophorinae, Anthophoridae), parasitic species are also relatively common.

Islands. The majority of the islands included in this survey are in tropical areas (e.g. Java, Cuba, Sri Lanka) and, as expected, have fewer parasites relative to islands at higher latitudes (e.g. Britain). As an extreme example, Ellesmere Island in the arctic has a bee fauna in which one of the two bee species is parasitic on the other (Appendix 1). Studies of island biogeography (MacArthur & Wilson, 1967) suggest additional complementary reasons why one might expect islands to have fewer parasites: (1) Parasites are likely to be poor colonists because suitable hosts must have already colonized the island (when speciation is allopatric); and (2) Parasite populations on islands, as on continents, are likely to be characterized by small size (e.g. Wilson, 1985), increasing the probability of chance extinction.

Montane regions. In temperate regions there are some similarities between increasing altitude and latitude (e.g. Mayr, 1963). Seasonal pollen profiles along a latitudinal gradient are similar to those from an altitudinal gradient, cf. Figs. 3 and 6 in O'Neil & Waller (1984). At higher altitudes in temperate regions (e.g. 'Suisse Romande' in Appendix 1), social parasites are relatively more abundant (also Wheeler, 1910; Wilson, 1971; Hamilton, 1972). High altitudes in the tropics, however, which are generally not more seasonal than lower altitudes (e.g. Lavery & Plowright, 1985), being relatively cooler the year round, are expected to have fewer parasitic species, although relevant data are lacking. Wheeler (1919) and Hamilton (1972) thought that disjunctions between host and parasite mating times, perhaps induced by development at varying altitudes (temperatures), might impose assortative mating and help explain the abundance of social parasites in north temperate montane regions. Temporal disjunctions, however, seem unimportant as species-isolating mechanisms in *Bombus* and *Psithyrus* (Svensson & Lundberg, 1977; Svensson, 1980; Bergström *et al.*, 1981).

X. THE RELEVANCE OF SEASONALITY AND HOST SYNCHRONY TO THEORIES ON THE EVOLUTION OF BROOD PARASITIC SPECIES

Parasitic bees, wasps and ants display tremendous diversity in morphology, behaviour, ovarian physiology, etc., yet are similar in being directly dependent upon other species for successful reproduction. This dependence requires that the life-cycles of individual parasites and hosts be synchronized, as for social queens and their workers.

Richards' (1927, 1953) ideas on the evolution of social parasitism in Hymenoptera have been well accepted (e.g. Wilson, 1971; West-Eberhard, 1986). Citing examples of facultative parasitism in bumblebees (*Bombus*), Richards suggested that it was a widespread phenomenon, and noted that obligate parasites (*Psithyrus* and some *Bombus*) have a north temperate biased distribution. He described a model to derive conditions under which the life-cycles of potential hosts are synchronized, while those of incipient parasites had a slight lag time. In this allopatric model of parasite speciation the ranges of a northern and an allied southern species overlap. In the more northern populations of the southern species there are individuals that emerge late, e.g. because cooler temperatures slow rates of development. These late emergers would have a

shortened season available for reproduction and, at a loss for time, they sometimes parasitize their northern congeners and so acquire parasitic behaviour. Subsequently they would evolve *obligate* parasitic behaviour, morphology, etc. Richards (1927), however, found no evidence suggesting southern species are facultative parasites of northern species in areas of sympatry more frequently than the reverse (Wilson, 1971, for wasps).

Commenting on Richards' ideas, Hamilton (1972) pointed out that some species of vespine wasps and bumblebees have migratory habits in northern temperate regions (also Mikkola, 1978, 1984) which would probably result in decreased genetic relatedness among individuals in a population. Varvio-Aho, Pamilo & Pekkarinen (1984) explain the lack of geographic variation at enzyme loci in some Finnish vespine wasps as a consequence of migrations swamping out local gene differences. Under these conditions, it is less likely that a conspecific neighbour host will be kin, and so any net cost to the host is of no consequence for the parasite (Hamilton, 1964, 1971; Gadgil *et al.*, 1983).

Matsuura & Yamane (1984) also proposed that obligatory parasitic behaviour is more likely to evolve in temperate regions. These authors considered social parasites, and suggested that *obligate* parasitism will evolve if the season available for colony growth is so short that any workers produced by a 'parasitic' queen are useless because of insufficient time to rear another brood. Conversely, in areas where the favourable season is longer, workers produced by a parasitic 'queen' will make a contribution to colony growth, and *temporary* parasitism will evolve.

Recent ideas on the evolution of behaviour and speciation (below) require that Richards' (1927-71) ideas on parasitism be modified along the lines that Richards (1971) himself suggested when he wrote that parasites might sometimes evolve "by the reverse of the process in which altruism is evolved". In temperate regions or in tropical areas where the breeding cycle is seasonally limited, the *relative* success of independent (free-living) reproductive behaviour probably *decreases* for late-starting individuals, while for parasitic behaviour it *increases*. This asymmetry in relative reproductive success is probably less pronounced in aseasonal areas or species, and helps explain why (facultative) parasitic behaviour becomes fixed more often within populations in temperate regions.

Ideas on the evolution of parasitism seem to mirror those on the evolution of eusociality. The conventional way of thinking about social evolution has been questioned by Michener (1985), who reviewed data on bees showing that individuals *within* populations of solitary species are sometimes facultatively eusocial, so that social behaviour often evolves without concomitant speciation (also West-Eberhard, in press; Evans & Hook, 1986 for wasps). These examples are specific cases of a general phenomenon described by West-Eberhard (1986), who emphasized the importance of conditional expression of alternative phenotypes for the evolution of new lineages. She cited the multiple evolutions of social parasitism in Hymenoptera as examples. West-Eberhard's (1986) model provides a mechanism by which a parasite lineage can evolve directly from a host/ancestor without requiring the existence of behaviourally intermediate species, and without requiring allopatric speciation, as repeatedly suggested long ago, although without modern terminology (e.g. Pérez, 1883, 1884; Wheeler, 1919; Popov, 1945).

The geographic distributions of obligate brood parasitic birds are relevant since such species are more abundant in tropical areas (Payne, 1977), opposite to the brood parasitic Hymenoptera. Facultative parasitism in birds is geographically widespread (Yom-Tov, 1980), and host synchrony is also thought to be important for the evolution of bird parasites (e.g. Hamilton & Orians, 1965; Emlen & Wrege, 1986). Nesting and breeding behaviour in many tropical birds is relatively synchronized (e.g. Skutch, 1976), as it is for temperate species, so the hypothesis presented in this paper may also be relevant for parasitic birds. Payne (1977) suggested that avian brood parasites are more abundant in tropical regions because these are areas where rates of nest predation are highest. Birds which lay eggs in more than one nest would escape localized predation, and one way to distribute eggs in this pattern is to parasitize other nests (Andersson, 1984).

Under certain circumstances social, physiological and environmental factors act together such that some individuals acquire parasitic behaviour, while others remain free-living. If there is geographic variation in the factors which favour the acquisition of a parasitic phenotype, then it is interesting that there is also parallel variation in the extent to which one of the alternatives becomes uniquely expressed in populations (i.e. a parasitic species). Several factors tend to vary together geographically, often following a latitudinal cline, which generate more ecological opportunities (*sensu* Dobzhansky, 1950) for congeneric (or -specific) parasites of bees, wasps and ants in temperate regions, and relate to synchrony of individuals within host populations, as summarized below:

(1) Favourable rates of parasitization are usually density-dependent and, consequently, will be enhanced where host populations are large. Ontogenetic synchrony increases abundance in a temporal sense (the Fraser Darling effect, Section V).

(2) Competition for nests and nesting sites is sometimes density-dependent and may be exaggerated in areas where ontogenetic synchrony was high (Section V).

(3) A 'season' favourable for reproduction tends to become shorter with increasing latitude (and altitude in temperate zones). Individuals which begin nesting late (e.g. because of delayed emergence or following nest destruction) in such areas will be more disadvantaged relative to equally late individuals in areas having longer-lasting reproductive periods (e.g. many tropical areas). Facultative parasitic behaviour is more likely to be advantageous in areas where the favourable period is short so that the penalty for being late (asynchronous) is severe for free-living females.

(4) At least for some wasps and bees, parasites are sometimes more successful when social hosts are monogynous rather than polygynous. For these groups some evidence suggests there is an increase in the frequency of polygynous colonies with decreasing latitude (e.g. Michener & Bennett, 1977; Ross & Matthews, 1982; Ross & Visscher, 1983; Matsuura, 1983).

In social insects the life-cycles of queens and their workers are synchronized, as are the life-cycles of parasites and hosts, because in both cases the former are dependent upon the latter for successful reproduction. Environmental factors imposing nesting synchrony on populations of ants, bees and wasps, in concert with biological factors, seem to facilitate the evolution of parasitic behaviour. These factors often follow a latitudinal gradient and help explain why parasitic species in these groups are more abundant in temperate zones and become less abundant in the tropics.

XI. SUMMARY

(1) The evolution of brood parasitic behaviour in bees, wasps and ants is related to factors which co-vary with the degree of ontogenetic synchrony of individuals within potential host populations.

(2) Examples are given showing that, in general, populations in temperate regions are more synchronized than are those in tropical regions.

(3) As a consequence of social and environmental factors, facultatively parasitic behaviour is commonly acquired by individuals of solitary or social species in various geographic areas.

(4) Obligate parasitic behaviour in bees, wasps and ants is proportionally more common in temperate regions. A review of some faunal surveys of bees gives a correlation of $r = 0.66$ ($N = 114$) between the percentage of parasitic species and the estimated latitude of the area surveyed.

(5) The relevance of these relationships to other ideas on the evolution of parasites is discussed.

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XIV. APPENDIX

Tabulation of data from faunal bee surveys for numbers of parasitic versus free-living species. Surveys are listed in decreasing order of latitude within biogeographic regions. Usually the species names given in the surveys were not synonymized with those in current use.

* The complete citation for this reference is not provided here, and can be found in Michener (1979).

† This survey excluded social Apidae.

Locality	Latitude	Number of free-living species	Number of parasitic spp.	Parasitic spp. Total spp.	References
Nearctic region					
Ellesmere Isl., Canada	80° N	1	1	0.50	*Richards (1973)
Maine, USA	45° N	155	44	0.22	*Mitchell (1960, 1962)
Wisconsin, USA	45° N	127	42	0.25	*Op. cit.
Mount Desert, Maine, USA	44° N	94	17	0.15	Procter (1946)
Vermont, USA	44° N	84	16	0.16	*Mitchell (1960, 1962)
Michigan, USA	43° N	309	96	0.24	*Op. cit.
New Hampshire, USA	43° N	113	30	0.21	*Op. cit.
New York, USA	43° N	237	83	0.26	*Op. cit.
Wyoming, USA	43° N	556	97	0.17	*Lavigne & Tepedino (1976)
George Reserve, Mich., USA	42.5° N	132	42	0.24	Evans (1986)
Massachusetts, USA	42.5° N	209	69	0.25	*Mitchell (1960, 1962)
Chicago, Illinois, USA	42° N	137	34	0.20	*Pearson (1933)
Curlew Valley (Utah & Idaho), USA	42° N	115	15	0.12	Bohart & Knowlton (1973)
Connecticut, USA	41.5° N	156	49	0.24	*Mitchell (1960, 1962)
Pennsylvania, USA	41° N	147	36	0.20	*Op. cit.
Rhode Island, USA	41° N	101	22	0.19	*Op. cit.
Illinois, USA	40° N	213	64	0.23	*Op. cit.
Indiana, USA	40° N	165	41	0.20	*Op. cit.
New Jersey, USA	40° N	156	29	0.16	*Op. cit.
Ohio, USA	40° N	150	39	0.21	*Op. cit.
Carlinville, Illinois, USA	39° N	224	72	0.24	*Robertson (1929)
Delaware, USA	39° N	13	0	0.00	*Mitchell (1960, 1962)
Maryland, USA	39° N	107	28	0.21	*Op. cit.
Washington, D.C., USA	39° N	71	28	0.28	*Op. cit.

Locality	Latitude	Number of free-living species	Number of parasitic app.	Parasitic spp.		References
				Total app.		
West Virginia, USA	39° N	89	23	0·21		*Op. cit.
Nevada Test Site, USA	37° N	61	6	0·09		Allred (1969)
Kentucky, USA	38° N	38	13	0·24		*Mitchell (1960, 1962)
Virginia, USA	38° N	201	61	0·23		*Op. cit.
California, USA	36° N	1574	346	0·18		*Moldenke & Neff (1974)
Tennessee, USA	36° N	129	35	0·21		*Mitchell (1960, 1962)
North Carolina, USA	35° N	392	128	0·24		*Op. cit.
South Carolina, USA	34° N	56	15	0·21		*Op. cit.
Channel Isl., California, USA	34° N	83	8	0·09		Rust, Menke & Miller (1985)
Alabama, USA	33° N	65	13	0·17		*Mitchell (1960, 1962)
Georgia, USA	33° N	295	66	0·18		*Op. cit.
Mississippi, USA	32·5° N	105	11	0·09		*Op. cit.
Hattiesburg, Miss., USA	31° N	91	11	0·11		*Michener (1947)
Florida, USA	28° N	196	62	0·24		*Mitchell (1960, 1962)
Archbold Biol. Station, Florida, USA	27·5° N	54	20	0·27		M. Deyrup, unpubl. (1987)
Neotropic region						
Cuba	22° N	33	10	0·23		Cresson (1865)
Cuba	22° N	84	21	0·20		*Alayo (1970)
La Estación de Biología, Chamela, Mexico	21° N	194	27	0·12		Ayala & Bullock, unpubl. (1986) (See Addendum)
Jamaica	18° N	55	14	0·20		Raw (1985)
Costa Rica	10° N	67	9	0·12		*Friese (1925)
Panamá	9° N	306	47	0·13		*Michener (1954)
Barro Colorado Isl., Panamá	9° N	70	6	0·08		*Schwarz (1934a, b)
Argentina	37° S	182	48	0·21		Friese (1908)
Mendoza, Argentina	33° S	168	63	0·27		*Jørgensen (1912)
Chile	35° S	317	32	0·09		Toro (1986)
Chile	35° S	64	9	0·12		Spinola (1851)
Ribeirão Preto, Brazil	21° S	182†	25	0·12†		Camargo & Mazucato (1984)
Oriental region						
Barrackpore, India	23° N	57	16	0·22		*Rothney (1903)
India, Burma, Sri Lanka	23° N	254	33	0·12		Bingham (1897)
Philippine Islands	15° N	214	37	0·15		*Baltazar (1966)
Sri Lanka	9° N	40	7	0·15		Bingham (1896)
Java	7° N	98	18	0·16		*Friese (1914)
Ethiopian region						
Nigeria	10° N	116	19	0·14		Medler (1980)
Congo basin (Kongobeckens)	5° N	62	6	0·09		Friese (1921)
Australian region						
Australia & South Pacific	25° S	1874	46	0·02		*Michener (1965)
Samoa	14° S	11	2	0·15		*Perkins <i>et al.</i> (1928)
New Guinea	5° S	161	22	0·12		Friese (1909)
Palearctic region						
Finland	65° N	136	68	0·33		*Elfving (1968)
Leningrad, USSR	60° N	136	34	0·20		Morawitz (1868)
'Volgo-Uralensis', USSR	60° N	207	46	0·18		Eversmann (1852)
Bashkir, USSR	53° N	261	67	0·20		*Nikiforuk (1957)
'Ukraine forest' (Suma, Chernigov & Kiev), USSR	49° N	204	41	0·17		Osychniuk (1964)
Sweden	62° N	155	57	0·27		Aurivillius (1903)
Sweden	62° N	—	—	0·27		See Janzon & Svensson (1984)

Locality	Latitude	Number of free-living species	Number of parasitic spp.	Parasitic spp.		References
				Total spp.		
Scandinavia	60° N	149	62	0.29		Thomson (1872)
Latvia	58° N	—	—	0.28		See Janzon & Svensson (1984)
Öland, Sweden	56° N	—	—	0.28		* <i>Op. cit.</i>
Aledal, Sweden	57° N	—	—	0.32		* <i>Op. cit.</i>
Denmark	56° N	164	54	0.25		*Jørgensen (1921)
Laesø Island, Denmark	57° N	32	12	0.27		Lomholdt (1972)
British Isles	56° N	149	54	0.27		*Saunders (1896)
Great Britain	56° N	—	—	0.26		See Janzon & Svensson (1984)
Hiddensee Island, FDR	54.5° N	44	18	0.29		Oehlke & Dylewska (1975)
Bremen, FDR	53.5° N	179	73	0.29		*Alfken (1939)
Oldenburg, FDR	53° N	55	22	0.29		Haeseler (1978)
Ireland	53° N	86	37	0.30		*Stelfox (1927)
Bedfordshire, UK	52° N	110	48	0.30		*Chambers (1949)
Northwest Poland	54° N	146	36	0.20		Adolph (1984)
Western Poland	52° N	195	61	0.24		Banaszak (1982)
Kampinos Natl Park, Poland	52° N	131	49	0.27		Banaszak & Plewka (1981)
Wolin Natl Park, Poland	53.5° N	60	15	0.20		Banaszak (1973a)
Poznan, Poland	52° N	104	28	0.21		*Banaszak (1973b)
Netherlands	52° N	233	89	0.28		*Benno (1969)
Federal Republ. Germany	51.5° N	420	148	0.26		*Stoeckert (1954)
Federal Republ. Germany	51.5° N	385	132	0.25		Westrich (1984)
Chobham Common, Surrey, UK	51° N	—	—	0.27		See Janzon & Svensson (1984)
Belgium	50.5° N	87	34	0.28		Crèvecoeur & Maréchal (1935)
Belgium	50.5° N	155	50	0.24		Jacobs (1904)
'Chalk grasslands', Limburg, Netherlands	50° N	189	72	0.28		Lefebvre (1984)
Northern France	50° N	278	84	0.23		*Cavro (1950)
Tübingen, FDR	48.5° N	136	50	0.27		Westrich (1980)
Kolner Bucht, FDR	47° N	195	71	0.27		*Aerts (1949)
Nassau, FDR	50° N	181	43	0.19		*Buddeberg (1895)
'East Prussia'	47° N	178	66	0.27		*Alfken (1912b)
'West Prussia'	47° N	235	76	0.24		* <i>Op. cit.</i>
'West Prussia'	47° N	199	75	0.27		Möschler (1938)
Switzerland	47° N	—	—	0.26		See Janzon & Svensson (1984)
Neuchâtel, Switzerland	47° N	203	58	0.22		*Beaumont (1955)
Parc National Suisse	47° N	156	43	0.22		*Beaumont (1958)
Suisse romande (Alps)	47° N	75	36	0.32		*Beaumont (1960)
France	46° N	367	68	0.16		Dours (1874)
France	46° N	603	164	0.21		*De Gaulle (1908)
Trieste, Italy	46° N	221	45	0.17		*Gräffe (1890)
Coastal Trieste, Italy	46° N	298	66	0.18		*Gräffe (1902)
Southwest France	43° N	400	116	0.22		*Pérez (1890)
Spain	40° N	908	277	0.23		*Ceballos <i>et al.</i> (1956)
Portugal	40° N	121	25	0.16		Diniz (1959)
Iran	32° N	200	27	0.12		Popov (1967)
Crete	32° N	70	12	0.15		Schulz (1906)
Palestine	30.5° N	141	21	0.13		Alfken (1938)

XV. ADDENDUM

An updated (1987) faunal list for bees at La Estacion de Biología Chamela was recently obtained from R. Ayala and S. Bullock. This list included an additional 20 free-living species not recorded in the original survey (see Appendix I), yet there were no additional parasitic species. This finding further supports the idea that lower diversity of parasitic bee species in tropical areas is not an artifact of a sampling bias.